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THE MORPHOLOGY AND RELATIONSHIPS OF
AUSTROBAILEYA

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With seven plates and three text-figures

INTRODUCTION

THE RELATIONSHIPS of this interesting genus have remained in doubt since it was first collected in 1929 by Kajewski on the Atherton Tableland in Northern Queensland. In his original description of the genus, White (11) stated:

"As Dr. Diels has done considerable work on the Magnoliales and allied groups, particularly those of the Papuan region, I sent specimens to him. He wrote me that he regarded the plant as undoubtedly belonging to the Magnoliaceae and allied to *Drimys*. He further suggested, though the fruits were unknown, that I should publish a provisional description in the account of Kajewski's collection. Unfortunately though Kajewski's specimens consist of several sheets of flowering specimens, the material has become extremely brittle in the process of drying with the result that the flowers are very difficult to soften and describe. It seems impossible also to section one of the carpels to see the number of ovules. Until living or spirit material of the flowers and ripe fruits can be obtained it will be impossible to place the plant in its correct botanical position. For the time being it is probably best placed at the end of the Magnoliaceae — even in a restricted sense — with position uncertain."

Subsequently, White modified this opinion in a letter written August 5, 1940 to Croizat: "Your letter of the 14th June to hand, and in reply I might state that when I was in England I spoke to Mr. Dandy at the British Museum, the recognized authority on the Magnoliaceae, about my *Austrobaileya*. I had, of course, only provisionally placed it in the Magnoliaceae. Specimens of the wood parts were examined at the Jodrell Laboratory by Dr. Metcalfe, and from floral structure and anatomy, we think there is no doubt the plant is a new family allied to Monimiaceae.

Dandy and I had intended to prepare a publication on it later on. I might have done something when I was over the other side, but the war upset plans a bit. It is most desirable, of course, that fruit should be found before it is raised to family rank."

Croizat (5) placed the genus in a new sub-family of the Dilleniaceae, viz., the Austrobaileyeae, and subsequently (6) in an independent family, the Austrobaileyaceae, without further discussion of its affinities.

It is evident, accordingly, that three different relationships have been suggested for *Austrobaileya*, 1. the Magnoliaceae, 2. the Monimiaceae and 3. the Dilleniaceae. The question whether the genus should be placed in one of these families or in an independent family of its own can be satisfactorily answered only by comprehensive morphological investigations of adequately preserved material. Through the efforts of Mr. L. J. Brass, and Mr. S. E. Stephens of the Department of Agriculture of North Queensland, we have succeeded in obtaining such material of the flowers and vegetative parts, collected at Lamonds Hill, close to the type locality of *Austrobaileya scandens* C. T. White.

MATERIAL EXAMINED

Our morphological investigations are based upon examination of the following material:

1. Isotype specimen of *A. scandens* C. T. White, *Kajewski 1269*, Arnold Arboretum.
2. Two isotype specimens of *A. scandens* C. T. White, *Kajewski 1269*, New York Botanical Garden.
3. Isotype specimen of *A. maculata* C. T. White (12), *White 10734*, Arnold Arboretum.
4. Stems and leaves of *A. maculata* C. T. White, *White 10734*, kindly sent by Mr. White.
5. Stems, terminal shoots and leaves of *A. scandens* C. T. White, collected and preserved in FAA fixative, *Brass 18160*.
6. Eleven herbarium specimens of *Brass 18160*.
7. Flowering shoots of *Austrobaileya*, preserved in FAA fixative, collected August 26, 1948 by Mr. Stephens in the Lamonds Hill area.

THE STEM

The largest scandent stem of *Austrobaileya*, *Brass 18160*, examined by us is 13 millimeters in diameter. Part of a transverse section of this stem is illustrated in *Plate I, Fig. 1*. The pith is composed of parenchymatous elements having thick, lignified, secondary walls. It is relatively homogeneous except for the presence of scattered cells having abundant starch and dark-colored phenolic material. In longitudinal sections, these cells are seen to occur in more or less extensive, vertically oriented files. The parenchymatous elements of the perimedullary region, *Fig. 1*, are slender, much elongated vertically, thick-walled and internally septate.

The cortex is composed of parenchymatous cells having thick, un lignified, primary walls and containing abundant starch and more or less calcium oxalate in the form of "crystal sand." A considerable number of the cortical cells also contain dark-colored phenolic material. In the outer cortex of young stems, before the development of an extensive periderm, conspicuous secretory cells, i.e., "ethereal oil cells," are visible. These idioblasts are more or less spherical and have a tenuous suberized inner membrane.

The eustele of the stem is composed of numerous discrete strands of primary xylem and phloem which are faced externally by thick-walled septate fibres. During enlargement of the stem, as seen in transverse sections, *Fig. 1*, these arcs of phloem fibres form parts of a composite ring of sclerenchyma; the widening intervening spaces between the arcs of fibres being bridged by the formation of sclerotic parenchyma. The conspicuous multiseriate rays of the secondary body, *Fig. 1*, extend outward from the parenchymatous interfascicular lacunae of the eustele and exhibit considerable flaring in the secondary phloem. As is so frequently the case in scandent stems, there is a relatively abrupt transition in the secondary xylem between an inner first-formed zone of denser tissue and a subsequently formed, more porous part having conspicuously larger vessels.

The cambium is of a relatively primitive type, containing long (up to 1500μ), extensively overlapping, fusiform initials. The derived sieve cells, vessel members and parenchyma strands are of equivalent lengths, but the imperforate tracheary cells, which elongate during maturation of the secondary xylem, are longer.

The parts of the secondary phloem between the flaring multiseriate rays, *Fig. 2*, are composed largely of alternating transverse bands of sieve cells and phloem parenchyma strands, the uniseriate rays being inconspicuous except where their cells contain dark-colored phenolic material. *The sieve cells have no companion cells.* Our observations regarding this important fact have been verified by Professor Katherine Esau to whom we sent preserved material for examination. The long, extensively overlapping sieve cells have numerous sieve plates in their lateral surfaces, those at the ends of the cells exhibiting no structural differences that might be interpreted as evidence of the presence of sieve tubes. There are no sclerenchymatous elements in the secondary phloem, all of the cells having primary walls only. Elongated secretory cells, i.e. "ethereal oil cells," are of sporadic occurrence.

The imperforate tracheary elements of the secondary xylem, *Fig. 3*, are of two types, 1. normal thick-walled tracheids which lose their living contents at maturity and 2. septate elements which contain several nuclei, more or less starch and dark-colored phenolic material. The former tracheary cells have numerous, conspicuously bordered pits (with included slit-like apertures) in both their radial and their tangential walls. However, the bordered pits fluctuate markedly in size in different tracheids, varying in diameter from 3μ to as much as 10μ . In the septate elements, the bordering areas of the pits fluctuate from conspicuous to vestigial.

The vessels of the secondary xylem range in size from diameters approximating those of the largest tracheids, i.e. 30μ , to diameters of as much as 200μ . All of the vessels regardless of size have scalariform perforation plates, but the form of the vessel members, and the number, size and character of the perforations changes markedly with increasing diameter of the vessels. In those of minimal cross-sectional area, the constituent cells are tracheid-like in form, i.e. fusiform with gradually tapered ends as seen in tangential longitudinal sections of the stem. The aggregations of scalariform bordered pits in the radial facets of the vessel members, *Fig. 5*, differ from those of scalariformly pitted tracheids only in the dissolution of pit-membranes in a number of the fully bordered pit-pairs. With increase in the diameter of the vessels, the perforated pit-pairs are reduced in number, greatly enlarged and lose most of their borders, compare *Figs. 5, 6 and 7*. In the case of the smaller vessels, the perforated pits occur in radial walls that are only slightly inclined to the long axis of the vessels, and therefore are fully visible in thick, radial longitudinal sections of the stem. On the contrary, during the ontogenetic expansion of large vessels, restricted parts of the radial facets, i.e. those in which perforations will ultimately be formed, assume an increasingly diagonal orientation, *Fig. 4*, and are fully visible in surface view, *Fig. 7*, only in sections cut at an inclination of approximately 45 degrees to the longitudinal axis of the stem.

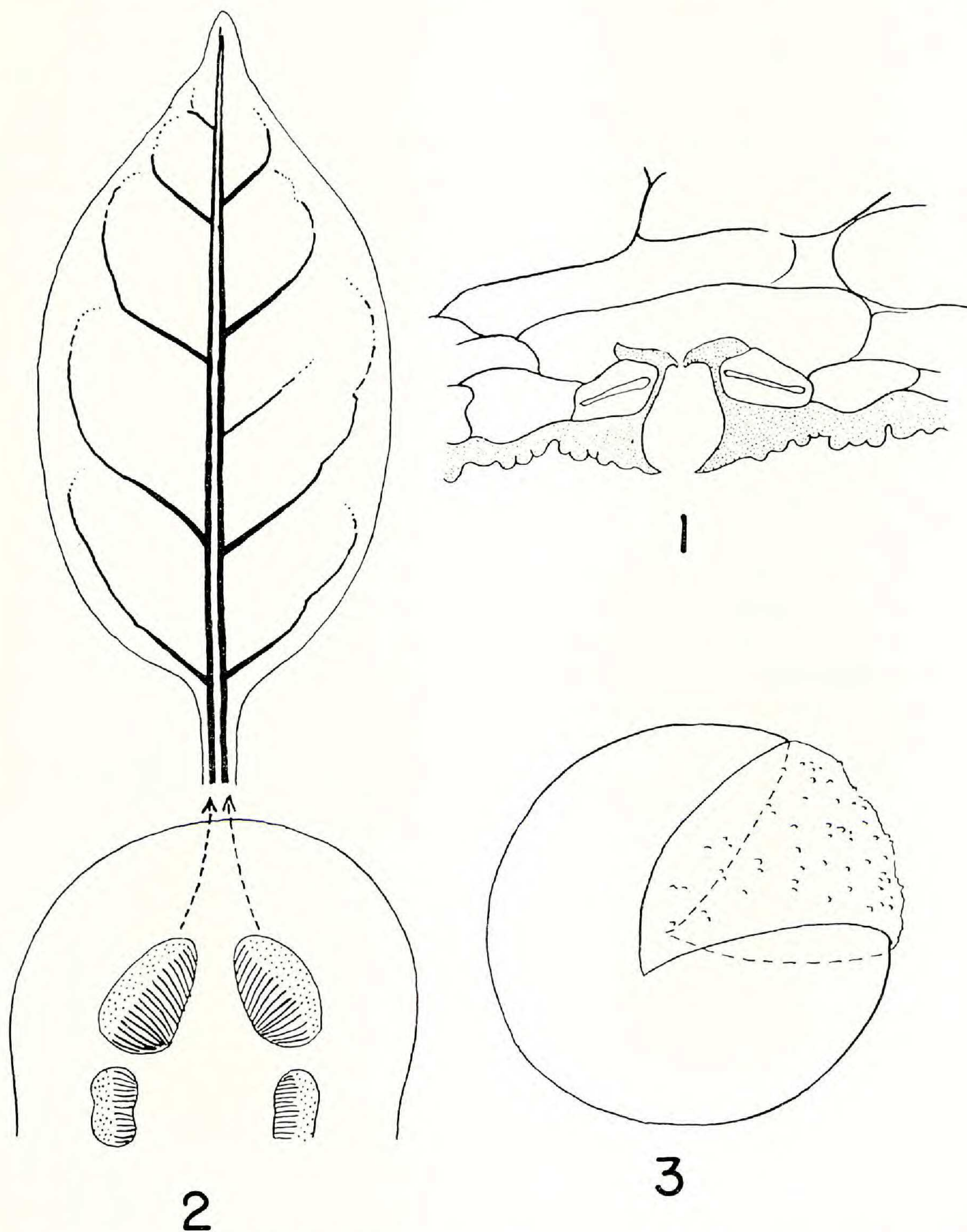
Most of the vessels are diffusely scattered, but a few of the larger ones occur in tangentially oriented pairs, *Figs. 1 and 3*. Where the vessels are in contact with tracheids, the imperforate bordered pits are relatively large and circular, where in contact with rays or wood parenchyma strands, the pits are smaller but clearly bordered. Where vessels are in contact laterally, the imperforate bordered pits are large, more or less transversely elongated and in opposite or alternating, multiseriate arrangement.

The wood parenchyma is paratracheal in distribution, *Fig. 3*, and, as frequently the case in scandent stems, tends to be more abundantly developed on the abaxial sides of the vessels. The multiseriate rays are extensive longitudinally, *Fig. 4*, having slender elongated cells on their flanks and high-celled uniseriate extensions on their upper and lower margins. The uniseriate rays exhibit evidences of phylogenetic reduction, particularly in the first-formed part of the secondary xylem, are low and composed of vertically much elongated cells.

THE LEAF AND NODAL ANATOMY

During early stages of the ontogeny of the vegetative shoot, the leaves are arranged in a typical decussate phyllotaxy. However, during subsequent growth of a shoot, the leaves of an individual pair may remain truly opposite or they may become sub-opposite or even widely separated by irregularities of interstitial elongation. The entire, glabrous, pinnately veined leaves are coriaceous at maturity, being provided with a thick and conspicuously striated cuticle in surface view. The relatively large

stomata of the lower surface of the leaf may have subsidiary cells oriented parallel to the guard cells ("syndetocheilic" or "rubiaceous" appearing type) or they may be surrounded by ordinary epidermal cells ("haplocheilic" type). In anticlinal sections, cut at right angles to the long



TEXT-FIGURES 1-3. *Fig. 1.* Section of a stoma from the under surface of a leaf, $\times 690$. *Fig. 2.* Diagrammatic representation of the transverse section of a node and the vascularization pattern of a leaf. *Fig. 3.* Mature pollen grain, $\times 982$.

axis of the stomata, *Text-fig. 1*, a highly characteristic pattern of cuticularization is revealed. There is a conspicuous vestibule in the thick cuticle, and the cuticular substance extends inward along the surfaces of the guard cells forming two massive plates which subtend them. There is no clearly defined hypodermis or palisade tissue in the mature leaf. More or less spherical secretory idioblasts, i.e. "ethereal oil cells," are scattered through the mesophyll, and are particularly conspicuous in young developing leaves. Many of the cells of the mesophyll contain dark-colored, phenolic substances.

Each leaf is vascularized (as are so many cotyledons of angiosperms) by two discrete strands that are related to a single gap in the eustele, *Text-fig. 2*. In other words, the nodal anatomy of *Austrobaileya* is of a *unilacunar* type. The detailed behavior of the two vascular strands fluctuates considerably in different mature leaves, even in those of a single plant. In certain of them, the two strands remain separate throughout the petiole and the costa of the lamina, each half of the lamina being vascularized by the ramifications of an independent system, *Text-fig. 2*. In other leaves, the two strands may be closely approximated or they may fuse to form a single arc, particularly in the middle and terminal parts of the mid-rib. It is significant in this connection, however, that during early stages of the ontogenetic development of leaves, there are two separate strands of procambium, subsequent approximations and localized fusions occurring during the differentiation of metaxylem or of secondary xylem and phloem. Below the node, the two foliar traces (when traced downward in serial transverse sections of the stem) remain independent of each other and become attached to two independent parts of the eustele. In other words, *the two leaf traces do not originate as a dichotomy of a single vascular bundle*.

In mature leaves, the smaller veins are jacketed by thick-walled fibres, but these fibres decrease in number toward the base of the mid-vein and commonly are absent in the petiole.

THE FLOWER

The flower buds of *Austrobaileya* are borne in the axils of leaves and are solitary in all specimens examined by us. Those collected by Mr. Stephens, are globose, *Figs. 8-10*, the pedicels varying from 0.5 to 1.0 cm. in length, depending upon the age of the bud. The short pedicels of young flower buds bear 8 to 10 pairs of decussately arranged bracts. Subsequently during interstitial elongation of the pedicel, the bracts of one or two of the central pairs tend to be displaced. Thus, in older buds it is common to find 2 or 3 pairs of compactly and decussately arranged bracts at the base of the pedicel, 2 or 4 more or less widely spaced bracts in the middle of the pedicel, and 2 or 3 pairs of compactly and decussately arranged bracts subtending the perianth, *Fig. 9*. The penultimate and ultimate pairs of bracts are larger and more woody than the rest, *Figs. 8-11*.

The perianth, as also the inner appendages of the flower, are arranged

on the floral axis in a much compressed spiral. There is no clearly defined differentiation of the perianth into calyx and corolla. In both species of *Austrobaileya*, the outermost tepal is somewhat larger than the subtending bracts. The central tepals of the series progressively attain larger dimensions, whereas the inner tepals become reduced in size to dimensions more nearly equivalent to those of the outer members of the series, *Figs. 20-32*. The tepals of *A. scandens*, *Kajewski 1269*, are much larger than those of *A. maculata*, *White 10734*, and the innermost ones tend to be of spatulate form.

The androecium of *A. maculata*, *White 10734* as of Stephens' collection, consists of 19 to 25 members, the outer 6 to 9 of which differentiate as stamens and the remainder as staminodia. The two categories merge into one another, one or two staminodia in the transition region not infrequently bearing degenerate sporangia, *Fig. 17*. The fertile male appendages are broad microsporophylls bearing protuberant sporangia on their conspicuously concave inner surface, *Figs. 15, 34, 36*.

The fertile microsporophylls and the staminodia of *A. maculata*, *White 10734* as of Stephens' collection, are characterized by having more or less numerous and conspicuously embossed purple spots, *Figs. 15-19* and *34*. These dark-colored areas tend to be more abundant on the staminodia than on the stamens, and on the adaxial than on the abaxial surface of the fertile microsporophylls. In the case of dried herbarium material, *White 10734*, the phenolic contents of the papillate epidermal cells, *Fig. 42*, of the purple areas turn black, and the spots become strikingly embossed, evidently through excessive contraction of surrounding tissue.

The stamens and staminodia of *A. scandens*, *Kajewski 1269*, are larger than those of *A. maculata*, *White 10734*, and differ from them in both form and texture, compare *Figs. 33* and *34*. They do not exhibit dark-colored embossed spots. Nor does Kajewski mention the occurrence of conspicuous purple areas in his field-notes on the color of freshly collected flowers.

The fact that the flowers collected by Mr. Stephens, close to the type locality of *A. scandens*, resemble those of *A. maculata* from Mt. Spurgeon raises the question whether there actually are two distinct species of overlapping ranges. Can the striking differences in size, form, texture and structure between the flowers of *A. scandens*, *Kajewski 1269*, and those of *A. maculata*, *White 10734* and Mr. Stephens' collection, be due to different developmental stages of the flowers at time of collection? In other words, is the larger size of the flowers of *A. scandens* and of their constituent parts due to the fact that the flowers were collected at anthesis, whereas those of *A. maculata* and the Stephens' collection had not attained their final stages of expansion? In order to answer this question, we have examined a young flower bud of *A. scandens*, *Kajewski 1269*, of approximately the same dimensions as the largest flower buds of *A. maculata*, *White 10734*. The stamens and staminodia of this immature flower exhibit the same differences in form and texture as the fully developed flowers, and do not have dark-colored embossed spots.

It should be noted in this connection, however, that the only conspicuous morphological difference between the vegetative organs of *A. scandens* and *A. maculata* is in the shape of the leaves. The internal anatomical characters of the stem and leaves are similar. The leaves of 11 duplicate sheets of *Brass* 18160 are of uniform elliptic to lanceolate form regardless of marked variations in size, and thus resemble those of *A. scandens*, *Kajewski* 1269. The "nitid" character of the latter collection is due apparently to over-heating during drying. The leaves of *A. maculata* are elliptic-ovate to ovate.

The staminodia of *A. scandens* and *A. maculata* are irregularly ridged or folded longitudinally, *Figs.* 17–19. As seen in transverse sections, their basal part is solid and the ridges extend in diverse directions, *Fig.* 36, whereas their apical parts are characteristically conduplicate, *Fig.* 35.

Above the insertion of the staminodia, the floral axis terminates in a broad mound on the surface of which the free carpels are borne, *Figs.* 12 and 38. In *A. maculata*, *White* 10734 and in Mr. Stephens' collection, the number of carpels ranges from 6–8, but as many as 14 may be present in *A. scandens*, *Kajewski* 1269. The dorsal outline of the carpel, *Fig.* 13, is more curved than the ventral surface which is nearly straight, the style being in line with the ventral side. The carpel has a more or less extensive solid basal part, *Figs.* 14 and 37, which may possibly represent a much modified stipe. The locule, situated in the dorsally more bulging part of the carpel, contains from 8 to 13 anatropous ovules in two series, *Figs.* 14, 37 and 44.

The carpels of *Austrobaileya* exhibit extreme phylogenetic modifications of the primitive conduplicate megasporophyll of the "Tasmania-Degen-eria" type, viz. 1. closure of the carpel, 2. differentiation of a hollow style and 3. elimination of the external, paired, stigmatic crests. Closure of the ovule-bearing part of the megasporophyll has progressed, as in the *Wintera* section of *Drimys*, Bailey and Nast (2), by concrescence of the stigmatic ventral surfaces of the conduplicate megasporophyll. Although closure by concrescence is complete externally, *Figs.* 36 and 44, evidences of the suture are preserved internally by a conspicuous cleft in the carpellary wall, *Fig.* 44. This cleft is jacketed by papillate cells that function in the downward extension of pollen tubes. Similar concrescence has occurred in the constricted stylar part of the primitively conduplicate megasporophyll, *Figs.* 45 and 46, forming a tubular extension whose cavity communicates with the locule, *Fig.* 37, and is lined by a more or less papillate and glandular appearing epidermis. The upper part of the style is bifid, *Fig.* 13. Just below the level of forking, the style is typically conduplicate and open on its ventral side. The ovules are anatropous and have two integuments, the outer being thicker, *Fig.* 44.

POLLEN

The wall of a young microsporangium of *A. maculata* in sectional view, *Fig.* 39, shows an epidermis subtended by three layers of wall cells which

are subtended in turn by a single, or an irregularly 2-layered, tapetum. When the microspore mother cells are undergoing reduction divisions, the tapetal cells become binucleate, *Fig. 40*. During later stages, the walls and the cytoplasm of the tapetal cells become homogeneously granulate and lose cellular organization, *Fig. 41*. However, neither an amoeboid shape of the individual cells nor their migration into the cavity of the sporangium, as often happens with the periplasmodial type of tapetal organization, was seen. The nutritive layer is soon absorbed after the stage represented in *Fig. 41*.

The microspore mother cells undergo reduction divisions in a simultaneous manner and form tetrads of microspores. The thickening of the exine commences while the microspores still cling together in tetrads. This feature facilitates observation of the differentiation of the germinal furrow on the distal face of the grain. The generative cell is cut off towards the furrow-end of the grain and the pollen grains are two-celled at the time of shedding.

The mature pollen grain is spherical with a single germinal furrow running nearly from pole to pole. The exine is thick and appears to be finely pitted, occasionally 3–5 pits being arranged in variously curved lines. The external surface of the furrow is sparsely flecked with minute protuberances, *Text-fig. 3*.

VASCULARIZATION OF THE FLOWER

The following observations upon the vasculature of the flowers of *Austrobaileya* are based largely upon preserved specimens collected by Mr. Stephens. They have been supplemented, however, by an examination of cleared carpels and stamens from herbarium specimens of *A. scandens*, *Kajewski 1269*, and *A. maculata*, *White 10734*.

At the base of the pedicel, there are 10–14 vascular bundles arranged in four independent aggregations, *Text-fig. 4*. The parenchymatous lacunae between these aggregations of bundles correspond with the decussate arrangement of bracts on the pedicel, i.e. four orthostichies. Each bract receives a pair of strands, the individual members of the pair arising from independent systems of the eustele, *Text-fig. 4, b1–b8*.

The vasculature of the tepals is similar to that of the bracts. The distinctness of the individual members of the pair of strands is particularly clear in the bases of the outer tepals, *t1–t10*; in the inner tepals, one of the strands of the pair is either feebly developed, *t11*, or altogether absent, *t14, t15*. Within the tepal, the two strands fuse and then split into a large number of veins that vascularize the lamina.

The stamens and staminodia may show at their point of attachment either two distinct vascular strands, or a pair of closely approximated strands, or a single strand. Usually in the outer functional microsporophylls, the strands are distinctly double at least at the base, *stn 1–stn 6*, while in the inner androecial members, a section at a corresponding level usually shows a single strand, *std 5–std 11*. However, when this strand

is followed downwards in the axis, it frequently is formed by the fusion of two bundles from independent systems, *std 9*, *std 10*, etc.

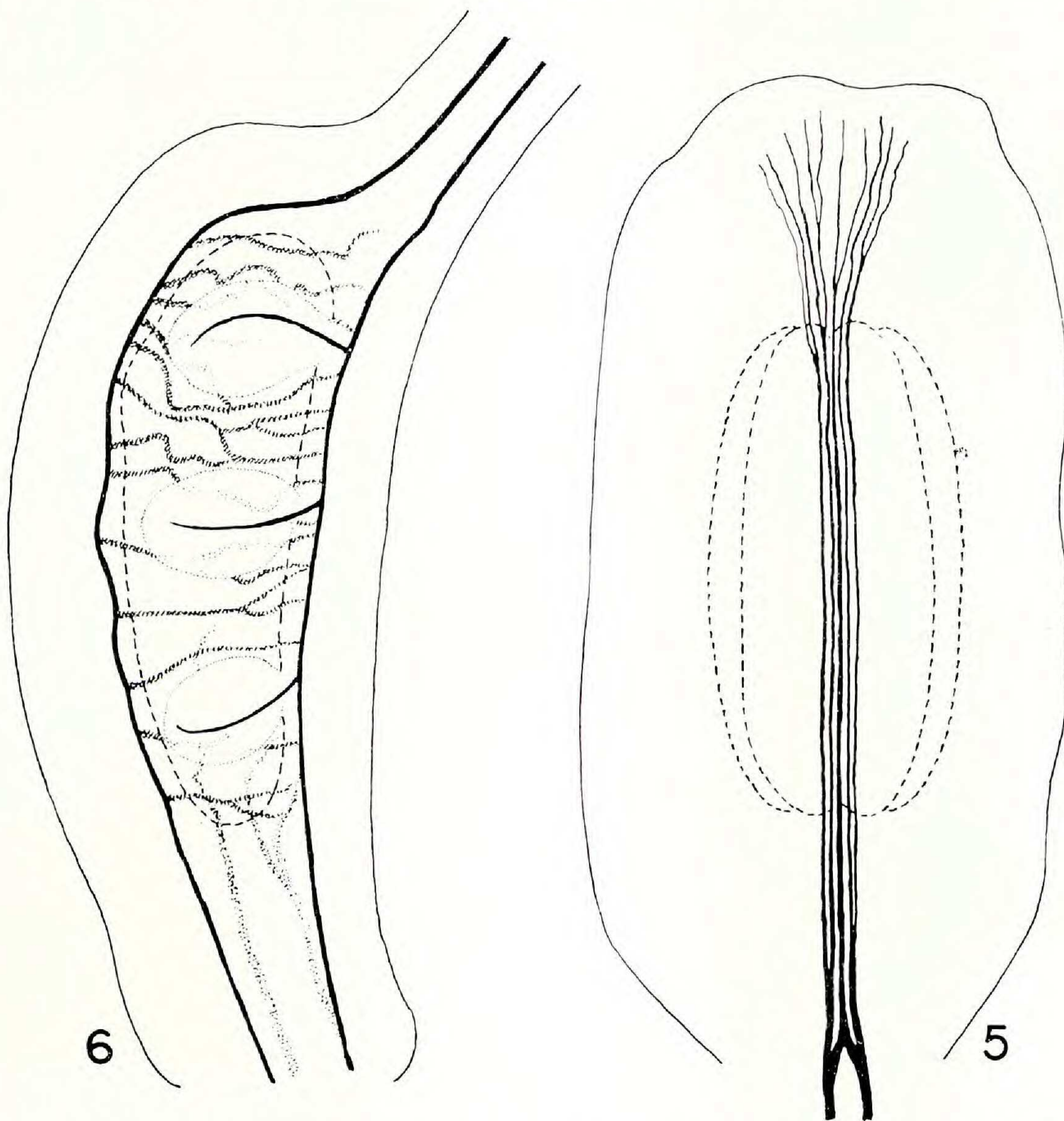
When a single vascular strand enters the microsporophyll, it soon trifurcates, the lateral strands again splitting at higher levels. On the other hand, when two strands supply the microsporophyll, they dichotomize at the base of the structure and the middle two branches fuse; the lateral branches also bifurcate at a slightly higher level, *Text-fig. 5*. In both instances, the strands remain close together as far as the level of the apexes of the sporangia and then spread in a fan-shaped manner.

In the case of flower buds collected by Mr. Stephens, the exact number and the behavior of the strands that enter the carpels could not be deter-



TEXT-FIGURE 4. Pattern of vascularization of a flower. The axis is shown as if longitudinally cut on one side and spread in one plane. *b1-b8*, bracts; *t1-t15*, tepals; *stn 1-stn 6*, stamens; *std 1-std 13*, staminodia; *C I-C VI*, carpels. The upward terminations of strands correspond approximately to the level of insertion of the respective appendage.

mined with certainty. Even in the oldest bud examined, *Text-fig. 4*, some of the vascular strands were still in the process of differentiation (indicated by stippled lines in the figure) and it is not possible at such a developmental stage to determine their true relationship either to the floral axis or to the carpels. However, in the buds examined by us, at least three vascular strands were well differentiated in most of the carpels. These strands occupied positions corresponding to the median and ventral veins. The median vein in some cases, *C I*, showed distinct doubleness at the point of entry into the carpel and when traced downwards, the two halves fused with two independent systems of bundles in the axis. In other carpels, the two strands gave indications of ontogenetic fusion,



TEXT-FIGURES 5, 6. *Fig. 5.* Vascularization pattern of microsporophyll; broken lines denote the position of the sporangia. *Fig. 6.* Vascularization pattern of carpel; broken line denotes the extent of the locule. Vascularization is shown in one longitudinal half of carpel which is cut in the plane of conduplication.

C III, C IV. In still others, the median strand had lost its paired appearance and its true double nature was demonstrable only far below in the axis, *C II, C VI.*

In the case of carpels from herbarium specimens, *Kajewski 1269* and *White 10734*, the vasculature appears to be well developed at anthesis. Three of such carpels showed a distinctly double median strand at the base, the halves of which fused at a higher level in the "stipe." In others, the corresponding strand was single. Along its course through the locular part of the carpel, the median strand sends out numerous branches laterally in a pinnate manner and the branches form a diffuse net-work within the carpellary wall; the ends of the branches usually anastomose with the ventral strands, *Text-fig. 6.* The extra strands that often enter the carpel from the axis also anastomose with the system of the median strand. The ventral strands supply the ovular traces and extend to varying distances in the style along with the median strand.

Taking the vascular pattern of the flower as a whole, it appears that although there may be considerable variation among the different appendages of the same flower, and even among those of the same whorl, the paired condition of the median strand is fundamental. In those instances where the strand appears single, it is often possible to demonstrate its double nature at lower levels of the floral axis. In other words, the doubleness of the median vascular strands of the floral appendages, as in the case of the vegetative leaves of *Austrobaileya*, is *not* a result of dichotomy of a single bundle, but of the approximation of two distinct strands originating from two separate systems of bundles.

DISCUSSION

The genus *Austrobaileya* has *monocolpate* pollen. This structural type of pollen occurs in many seed ferns, Bennettitales, Cycadales, Ginkgoales, monocotyledons and in certain families of the Ranales (*sensu lato*), Bailey and Nast (1), Swamy and Bailey (13). The rest of the dicotyledons, including the Dilleniaceae, have *tricolpate* pollen or phylogenetically modified types of such pollen. Thus, the occurrence of monocolpate pollen in *Austrobaileya*, coupled with the presence of "ethereal oil cells" and the absence of raphides, precludes any close relationship of the genus to the Dilleniaceae.

Among families of general ranalian affinities which have monocolpate pollen (or phylogenetically modified types of such pollen) all have "ethereal oil cells" of a characteristically similar type with the exception of the Cabomboideae and the Nymphaeoidae of the Nymphaeaceae. These secretory cells and monocolpate pollen occur in association in *Austrobaileya* which indicates that the genus belongs among this complex of families rather than among ranalian families having tricolpate pollen, viz. Trochodendraceae, Tetracentraceae, Eupteleaceae, Illiciaceae, Schisandraceae, Cercidiphyllaceae, Ranunculaceae, Berberidaceae, Lardizabalaceae or Menispermaceae.

The nodal anatomy of *Austrobaileya* is of a *unilacunar* type. Among ranalian families, having monocolpate pollen (or modified forms of such pollen) and "ethereal oil cells," this form of nodal structure occurs in the Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Lactoridaceae and Chloranthaceae (*Ascarina* and *Hedyosmum*). On the contrary, the Winteraceae, Degeneriaceae, Himantandraceae, Magnoliaceae (sensu stricto), Annonaceae,* Eupomatiaceae, Myristicaceae,* Canellaceae, Piperaceae, and Saururaceae have dominantly *trilacunar* or *multilacunar* nodes or anomalous nodal structures, e.g. the Calycanthaceae.

Not only does *Austrobaileya* differ from the Winteraceae, Magnoliaceae, Annonaceae and other more or less closely related trilacunar and multilacunar ranalian families in its nodal anatomy and in the vascularization pattern of its leaves and floral appendages, but also in the structure of its xylem and phloem, its parenchymatous and sclerenchymatous tissues and in the form and internal structure of its floral appendages. The *totality* of general morphological, and of specific anatomical, evidence is not indicative of relationship to any of these families (i.e. except distantly as members of a common ranalian grouping), but rather to the assemblage of unilacunar families enumerated in the preceding paragraph.

Among these unilacunar families, the Monimiaceae are the most highly diversified, exhibiting numerous trends of morphological and anatomical specialization, in both their vegetative and reproductive parts, and affording significant clues regarding phylogenetic changes that occurred in the evolution of the Gomortegaceae, Lauraceae, and Hernandiaceae.

Austrobaileya is a vine and there is a scandent tendency in a number of the Monimiaceae. The simple, pinnately veined leaves of *Austrobaileya*, as of the Monimiaceae and Chloranthaceae, are opposite or sub-opposite and exhibit a typical decussate phyllotaxy at least during the earlier stages of the development of a shoot. The leaves of *Austrobaileya*, as of *Trimenia* and *Piptocalyx* of the Monimiaceae, *Lactoris* of the Lactoridaceae and *Ascarina* of the Chloranthaceae, are vascularized by two strands that are independent at the nodal level of the stem and are attached at lower levels to independent parts of the eustele. The stomata of *Austrobaileya*, as of many Monimiaceae, are transitional between "syndetocheilic" and "haplocheilic" appearing, and have a similar pattern of internal cuticularization, Money (7). The xylem of *Austrobaileya*, as we have shown, Figs. 5-7, has numerous transitional stages in the development of vessels from tracheids with unusually large bordered pits. Such imperforate tracheids occur in the vesselless xylem of *Amborella*, Bailey and Swamy (4). Furthermore, there are numerous transitions between tracheids and septate fibres, such as are characteristic features of many Monimiaceae. In addition, calcium oxalate is deposited in *Austrobaileya*, as in the Monimiaceae and the Lauraceae, in the form of numerous minute crystals, viz. in the form of "crystal sand" rather than as conspicuous druses or large, single, rhombic crystals.

* Mistakenly reported as unilacunar by Sinnott (10).

The totality of available evidence from all vegetative parts of *Austrobaileya* provides no significant evidence for excluding the genus from the Monimiaceae as constituted by Perkins (8), particularly if such genera as *Amborella*, *Trimenia* and *Piptocalyx* are retained within the family. It is the flower of *Austrobaileya* and specifically its multiovulate carpels that is the chief obstacle to such a procedure. It should be noted in this connection, however, that there is such a wide range of morphological variability in the stamens, staminodes and carpels of the Monimiaceae that excessive emphasis should not be placed upon differences in the external forms of these organs in *Austrobaileya*. Furthermore, the tribes Hortonieae and Trimenieae were obviously established for florally more primitive representatives of the family, specifically for genera having free perianth members and a broadly convex or only slightly concave torus. Therefore, it would not appear to be entirely illogical to include in the family a genus which has retained broad microsporophylls and carpels in which the ovules have not been reduced to one, particularly as the vesselless *Amborella* is considered to be a member of the family.

As stated by us in a previous paper, Bailey and Swamy (4), if such genera as *Trimenia*, *Piptocalyx* and *Amborella* are to be retained in the Monimiaceae then the present concept of the family could be broadened to include *Gomortega* and *Austrobaileya*. Conversely, if a narrow concept of the family is to be maintained, then *Trimenia*, *Piptocalyx* and *Amborella* should be excluded, as well as such genera as *Gomortega* and *Austrobaileya*. However, before such decisions are attempted, it is essential to assemble more comprehensive and reliable information regarding *Gomortega*, *Austrobaileya* and the various genera of the Monimiaceae. As stated by White, in passages quoted in the introduction to this paper, it is essential to study the fruits and seeds of *Austrobaileya* before attempting to segregate the genus in an independent family. Mr. Stephens is attempting to obtain fruits and seeds for us, and, in addition, material suitable for critical embryological and cytological investigations. The separation of *Amborella* in an independent family, the Amborellaceae, Pichon (9), upon the basis of our preliminary note (3), without waiting for the publication of our detailed investigation (4), was premature and singularly unfortunate since erroneous statements regarding the ray structure and orthotropous character of the ovule were included in the brief description of the new family.

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EXPLANATION OF PLATES

PLATE I. *A. scandens*, Brass 18160. *Fig. 1.* Part of a transverse section of a large stem, $\times 20$. *Fig. 2.* Secondary phloem of same more highly magnified, $\times 130$.

PLATE II. *A. scandens*, Brass 18160. *Fig. 3.* Secondary xylem of *Fig. 1* more highly magnified, $\times 130$. *Fig. 4.* Tangential longitudinal section of the secondary xylem, $\times 50$.

PLATE III. *A. scandens*, Brass 18160. *Figs. 5-7.* Scalariform perforation plates of three vessels of different diameter, $\times 510$.

PLATE IV. *A. maculata*, Stephens' collection. *Figs. 8, 9.* Flower buds, $\times 3$. *Fig. 10.* Same, as seen from the stalk-end, $\times 3$. *Fig. 11.* Group of stamens and other inner appendages after the removal of the perianth, $\times 5$. *Fig. 12.* Group of carpels after the removal of the other floral appendages, $\times 5$. *Fig. 13.* Carpel, $\times 12$. *Fig. 14.* Same, longitudinal section passing through the plane of conduplication, to show the "stipe," locule and ovules, $\times 22$. *Figs. 15, 16.* Adaxial and side views of fertile microsporophyll, $\times 8$. *Figs. 17-19.* Staminodia; in *Fig. 17*, the structure bears degenerate sporangia, $\times 8$. *Figs. 20-32.* Perianth members of a single flower. The order from the outermost to the innermost runs according to the serial numbers, $\times 1$.

PLATE V. *Fig. 33.* *A. scandens*, Kajewski 1269. Stamen (middle) and staminodia (right and left), $\times 5$. *Fig. 34.* *A. maculata*, White 10734. Stamens (right and left) and staminodia (middle), $\times 5.5$.

PLATE VI. *A. maculata*, Stephens' collection. *Fig. 35.* Transverse section of a flower bud at the apical region, $\times 50$. *Fig. 36.* Same, at a central level, $\times 50$.

PLATE VII. *A. maculata*, Stephens' collection. *Fig. 37.* Longitudinal section of two carpels, the left hand one cut in the plane of conduplication, and the right hand one, at right angles to the previous plane, $\times 50$. *Fig. 38.* Longitudinal section of the floral apex, $\times 50$. *Figs. 39-41.* Structure of the microsporangium and tapetal organization, $\times 130$. *Fig. 42.* A portion of the epidermis of the microsporophyll, showing the histology of the pigment cells, $\times 130$. *Figs. 43-46.* Transverse sections of a carpel cut at successively higher levels, $\times 100$.

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